

Spatio-temporal Dynamics in the Origin of Genetic Information

Pan-Jun Kim , Hawoong Jeong *

*Department of Physics, Korea Advanced Institute of Science and Technology,
Daejeon 305-701, South Korea*

Abstract

We study evolutionary processes induced by spatio-temporal dynamics in prebiotic evolution. Using numerical simulations we demonstrate that hypercycles emerge from complex interaction structures in multispecies systems. In this work we also find that ‘hypercycle hybrid’ protects the hypercycle from its environment during the growth process. There is little selective advantage for one hypercycle to maintain coexistence with others. This brings the possibility of the outcompetition between hypercycles resulting in the negative effect on information diversity. To enrich the information in hypercycles, symbiosis with parasites is suggested. It is shown that symbiosis with parasites can play an important role in the prebiotic immunology.

Key words: prebiotic evolution, complex networks, self-structuring

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1 Introduction

The appearance of a molecule which is capable of replicating itself is probably the most fundamental event in the history of life. One of the candidates for the prebiotic genes, RNA is both the carrier of genetic information and the molecule with biological activities of which variety becomes an interesting topic recently [1]. Eigen and coworkers were the first to address the existence of the information threshold in prebiotic evolution that the length of a molecule (polynucleotide) is limited due to the finite replication accuracy per nucleotide [2]. The maximum length of the molecules attained by the process of Darwinian

* Corresponding author. Tel:+82-42-869-2543; fax:+82-42-869-2510.

Email address: hjeong@kaist.ac.kr (Hawoong Jeong).

URL: <http://stat.kaist.ac.kr/~pj/origin.html> (Pan-Jun Kim).

selection seems to be too short for a genetic message to encode a functional protein. In their hypercycle theory Eigen suggests that if molecules catalyze the replication of each other in a cyclic way, the information threshold can be crossed [2]. No molecule in the hypercycle can outcompete another because they are forced to cooperate. Each molecule is still bound to the maximum string-length, but the molecules can combine their information and thus the information threshold can be crossed.

However, there are two major problems with this idea. The first problem is that hypercycles with five or more species show a limit cycle behavior. This implies that large hypercycles are unstable because some species may become extinct. The second problem is that providing catalytic support to other species is in fact an altruistic behavior, therefore, they are extremely vulnerable to the presence of parasites which are species that do not reciprocate the catalytic support they receive.

Boerlijst and Hogeweg [3] have shown that spatial self-structuring can solve these extinction and parasite problems. They added the diffusive behavior of each species to the early model of hypercycle. In this spatially diffusive model, hypercycles with five or more species spontaneously generate spiral waves, rotating pattern of all species in the hypercycle. With the help of this rotating spiral wave global extinction of species no longer takes place. Furthermore, it turns out that spiral waves are resistant to parasite invasions. Because the molecules in the center of a spiral generate an offspring of the entire spiral in radial direction, it is difficult for a parasite to grow towards the center of the spiral.

Their pioneering work presents three important points. First, natural selection is effectively driven by spatio-temporal dynamics [3,4,5,6], not only by the population-driven competition between species. For example, Boerlijst and Hogeweg observed that increasing of diffusion rate makes the spiral patterns bigger, enhancing the resistance to invasion of parasites. Second, as a consequence of self-structuring, natural selection occurs at the level of the community but not of the individual [7]. A community maintains some minimum level of integrity for a long period enough for natural selection to act on. Integrity can be maintained as a form of nonrandom pattern in the spatial arrangement of individuals. Each spiral behaves like super-organism whose boundary is determined by the molecules in the periphery. Therefore the evolutionary attractors do not convey a fitness benefit to individual species but to the community determined by the spiral [4,8]. Third, they showed spatio-temporal dynamics of interaction networks can bring out nontrivial behaviors. The hypercycle which consists of a single cyclic interaction structure seems to be fatal to parasite invasions, but it turns out that the hypercycle is very robust when we consider its spatio-temporal dynamics. However, little is known about spatio-temporal dynamics for the case of more complex interaction networks

in this respect, while many research groups have studied several properties of complex networks recently [9,10].

In this paper, we addressed several issues which should be resolved to fully understand the spatio-temporal dynamics of multispecies interaction network. Boerlijst and Hogeweg let parasite invade hypercycles after full development of their spatial structures. But if parasite-like species is present before self-structuring of hypercycles, can hypercycles successfully drive away their initially embedded parasites? Also, if the multispecies system has the complex interaction structure (network) rather than a single cyclic structure as in the hypercycle model, is it possible that some cyclic sub-structures outcompete other sub-structures by the process of spiral-formation? We expect that the complex interaction structure would be separated into many cyclic sub-structures by self-structuring at first. And then competition between these cyclic sub-structures would select sub-structure with more efficient species. Our scenario on prebiotic evolution is different from that of Jain and Krishna [11,12] in which selection on species in the same giant structure containing autocatalytic sets is suppressed during structure development. In their scenario, evolutionary instability is unavoidable by a collapse of the giant structure due to the selection at the level of individuals in the complex interaction network.

In the next section we investigate the competition between initially embedded parasites and hypercycles and find the mechanism of separation of cyclic sub-structures using a simple model structure. Using numerical simulations, in Section 3 we demonstrate an emergence of information communities in prebiotic evolution. And we find that the ‘hypercycle hybrid’ protects the hypercycle from its environment during the development process. In Section 4 by investigating interaction between developed communities we find that self-interest of each community can discourage inheritance of diverse information. To recover information diversity, in Section 5 we introduce symbiosis with parasites and show that these embedded parasites can play an important role on the immunology of the community. The final section is devoted to conclusions.

2 Simple Trials

To study the spatio-temporal dynamics of hypercycles we use the following model equation [13].

$$\frac{dX_i}{dt} = -\delta_i X_i + (1 - \sum_{k=1}^N X_k)(\rho_i + \sum_j \kappa_{i,j} X_j) X_i + D_i \nabla^2 X_i .$$

We assume there are N different types of species and X_i denotes the concentration of species i at a given site. δ_i stands for the spontaneous decay rate of species i , ρ_i for the self-replication rate, and D_i for the diffusion coefficient. $\kappa_{i,j}$ is the rate of replication of species i catalyzed by species j . The first (second) term of rhs corresponds to the decay (growth) rate of population of species. The term $(1 - \sum_{k=1}^N X_k)$ limits the population of species at the same site due to finite resources. The final term shows diffusive behavior of species i which is responsible for spatial pattern formation. For numerical simulations we use a rectangular grid of 147×147 sites with Neumann boundary conditions. And we assume that species i is extinct when X_i is small enough (e.g., $X_i < 10^{-3}$). We use the integration time step $D_{max}\Delta t/(\Delta x)^2 = 0.1$ where we choose D_{max} as the maximum value of D_i ($i = 1, 2, \dots, N$), $\Delta x = 1$. We use the parameters $\delta_i = 1$, $\rho_i = 2$, $D_i = 1$, $\kappa_{i,j} = 0$ or 500 (depending on the existence of catalytic support to species i from species j) unless specified [14].

One necessary condition for cyclic sub-structures being favored in complex interaction structure would be the stability of the cyclic structures to initially embedded parasites. To investigate this stability we consider the structure in Fig. 1(a). Each arrow indicates the direction of catalysis, e.g. $2 \rightarrow 3$ means that species 2 catalyzes the replication of species 3 and, therefore concentration of species 3 increases. Species 7 is a parasite because it does not reciprocate the catalytic support given by species 6. We study the following two cases. First, to test whether hypercycles can drive away initially embedded parasites, we start with randomly assigned initial concentration containing molecules of all species (case A). Second, as a comparison with the situation where parasites invade hypercycles after fully development of spatial structure, we begin with randomly assigned initial concentration of six species while parasite concentration remains zero. And after spirals are fully developed, species in a half of the sites are replaced by parasite species (case B) [15].

By numerical simulations it is identified that initially embedded parasites are also effectively outcompeted although it is only possible in the narrow parameter region when compared with case B (see Fig. 1(b)). It turns out that even if parasites are initially embedded, spiral cores avoiding infection of parasites in the early stage can drive away the parasites by radial growth of the spiral waves (see Figs. 2(a-c)).

Next, we consider the structure in Fig. 3(a) where species 7 is equivalent to species 1 in their parameters. Separation of the cyclic sub-structures is successful by the spiral formation from molecules with randomly assigned concentration (see Fig. 3(b)). There are two kinds of spirals. One is composed of $1 \rightarrow 2 \rightarrow 3 \rightarrow 4 \rightarrow 5 \rightarrow 6 \rightarrow 1$ and the other is composed of $7 \rightarrow 2 \rightarrow 3 \rightarrow 4 \rightarrow 5 \rightarrow 6 \rightarrow 7$. Species 1 and 7 cannot coexist in the same spiral because the species (either 1 or 7) slightly out of the spiral core fails to invade the spiral core and is washed out from its environment (see Figs. 4(a-c)). As a result

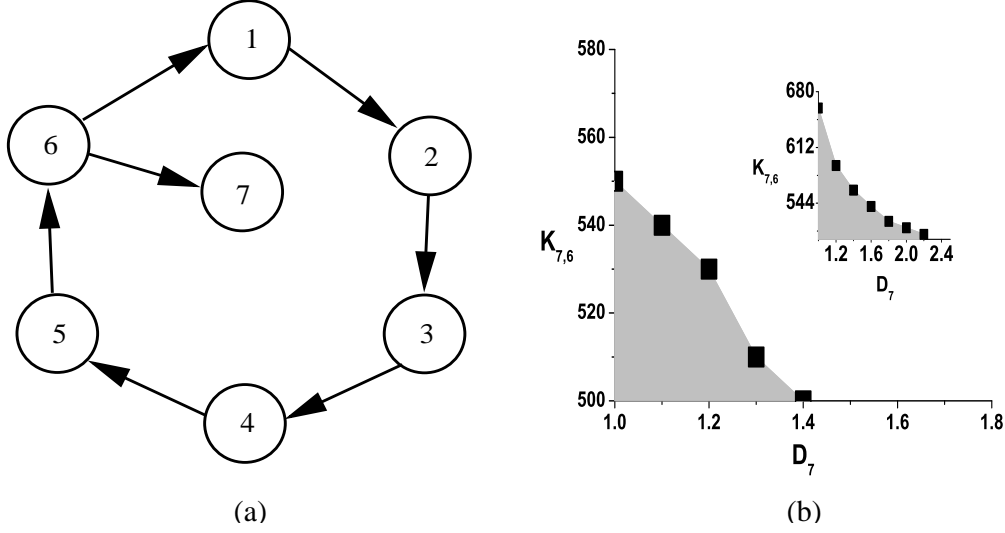


Fig. 1. (a) Schematic diagram of a hypercycle with the parasite-like species 7. (b) Phase diagram for the case A (inset for the case B). The horizontal axis for D_7 , the vertical axis for $\kappa_{7,6}$. Shaded area below the filled squares corresponds to the phase where parasite species is outcompeted. Refer to the main text for the case A and B.

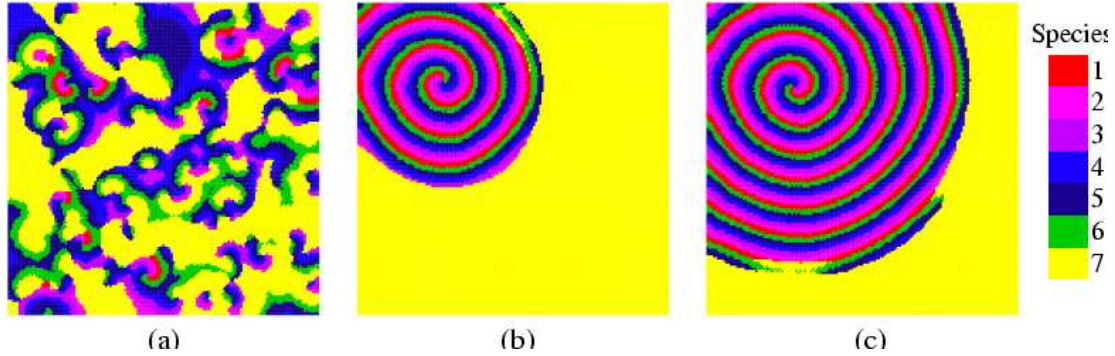


Fig. 2. Development of a spiral wave pattern with $D_7 = 1$ and $\kappa_{7,6} = 530$ in the case A. Painted with the color corresponding to the species which has the larger population size than any other species at a given site. Following pictures for spatial patterns are painted by the same method. (a) $t = 10$ (b) $t = 100$ (c) $t = 200$.

species 1 and 7 cannot coexist in the same spiral except for the case where two kinds of spirals come in contact with each other at peripheries. But even in that case separation at the level of spiral cores is clear (see Fig. 3(b)) and separation of cyclic sub-structures is completed.

In this section we examined the stability of the spiral against parasites in early stage, and explored the possibility that the specific cyclic sub-structures can be favored in the complex interaction networks.

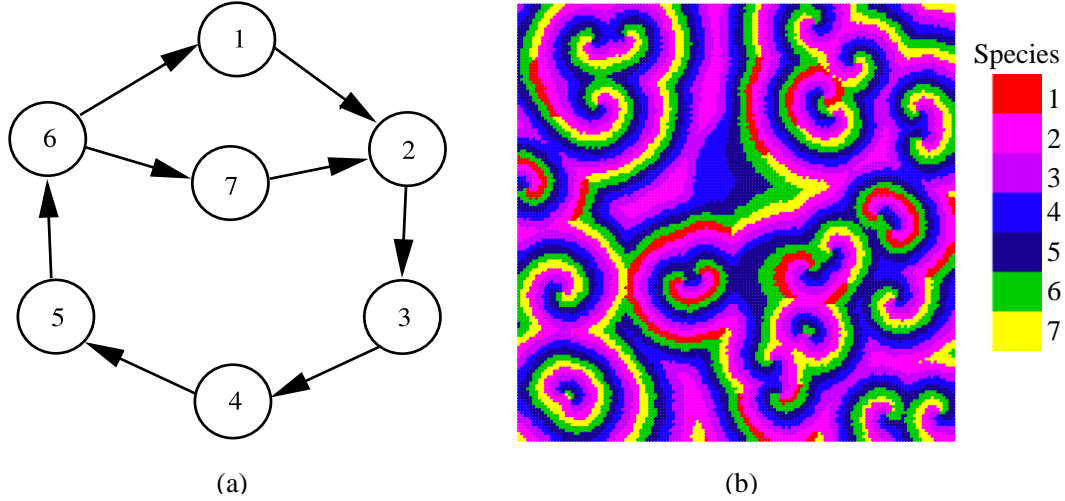


Fig. 3. (a) Schematic diagram of simply entangled hypercycles. (b) Development of two different spirals from entangled hypercycle network.

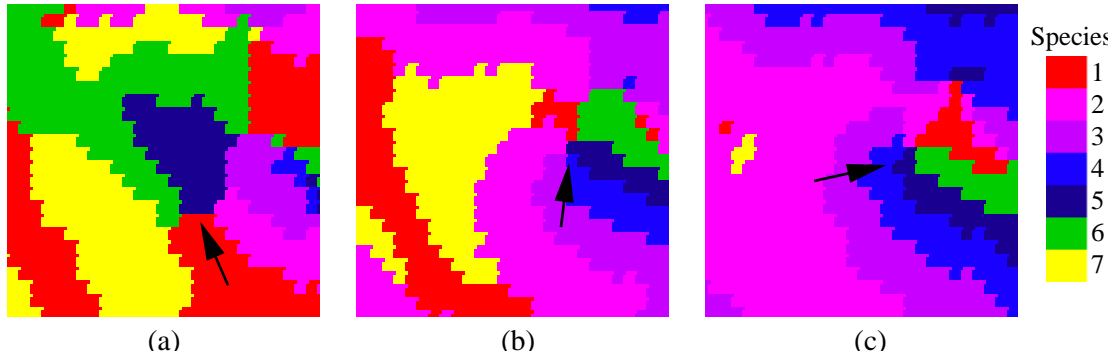


Fig. 4. (a) Competition between two cyclic sub-structures. Magnified pattern near the spiral core, at $t = 3$. The arrow in the figure indicates the spiral core with $1 \rightarrow 2 \rightarrow 3 \rightarrow 4 \rightarrow 5 \rightarrow 6 \rightarrow 1$. Species 7 is slightly out of the core. (b) At $t = 5$ species 7 cannot invade the spiral core. (c) At $t = 6$ species 7 is washed out by the environment.

3 Emergence of Communities

Next, we consider more complex model structure as in Fig. 5(a). There are three cyclic sub-structures, $1 \rightarrow 6 \rightarrow 5 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$, $1 \rightarrow 6 \rightarrow 7 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$ and $1 \rightarrow 6 \rightarrow 7 \rightarrow 8 \rightarrow 2 \rightarrow 1$. As expected in the previous section the cyclic sub-structure repels other sub-structures and each cyclic sub-structure coexists in the form of spirals. Each spiral can be considered as community where species in the same cycle mainly interacts each other.

However, it is unlikely that every parameters of each species will have the same value as system gets complex. We demonstrate that selection process indeed acts on these cyclic sub-structures due to species dependent parameters. If we increase the diffusion coefficient of species 5 by $D_5 = 2$, it is observed that

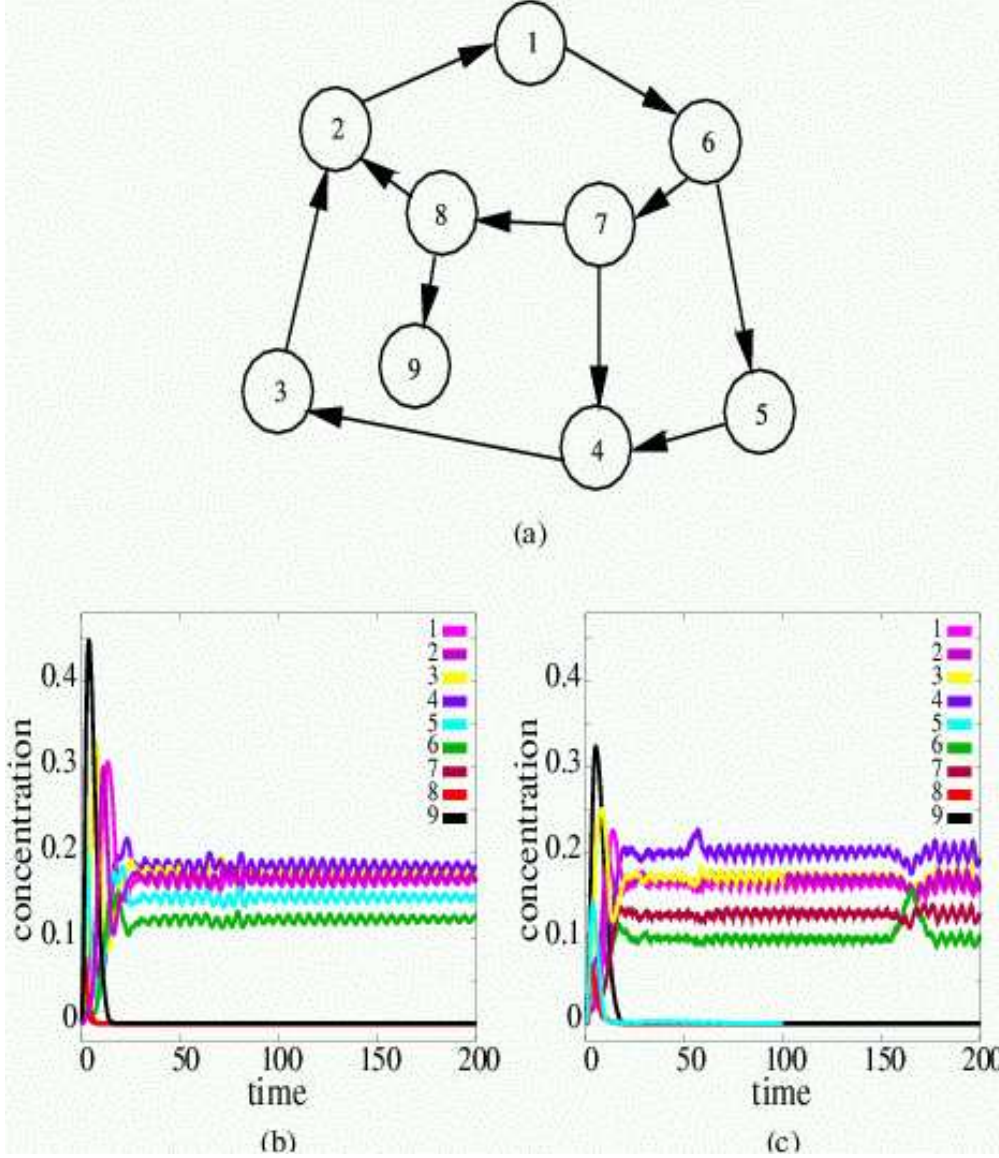


Fig. 5. (a) Schematic diagram of the model structure. Population of each species after local changes, where the horizontal axis is for evaluation time, the vertical axis for concentration of species averaged over the total sites. (b) When $D_5 = 2$ the species in $1 \rightarrow 6 \rightarrow 5 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$ are populated while the rest of species become suppressed. (c) When $\kappa_{7,6} = \kappa_{4,7} = 1000$ the species in $1 \rightarrow 6 \rightarrow 7 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$ are populated while the rest of species become suppressed.

$1 \rightarrow 6 \rightarrow 5 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$ outcompetes other cyclic sub-structures (see Fig. 5(b)) [16]. If we increase the catalytic support from species 6 to species 7 and from species 7 to species 4 by $\kappa_{7,6} = \kappa_{4,7} = 1000$, $1 \rightarrow 6 \rightarrow 7 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$ outcompetes other cyclic sub-structures (see Fig. 5(c)). As you can see, small variation in local parameter can change whole dynamics.

We note that selection occurs at the community level but not at the individual level because the individual-level selection is overridden by community [7]. In

the situation of Fig. 5(c), the species 6 gains little benefit in $1 \rightarrow 6 \rightarrow 7 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$ cycle because of its altruistic behavior in this community (see the population of species 6 in Fig. 5(c)). But since the species 6 enhances the fitness of the entire community, the species 6 involved in $1 \rightarrow 6 \rightarrow 7 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$ is selected in the final stage rather than the species 6 in $1 \rightarrow 6 \rightarrow 5 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$.

In the above example, we observed competition between cyclic sub-structures and resulting selection process. From these observations we find that we don't need to affect overall properties of the entire community to select a particular community. We just need to adjust local properties of the interaction, e.g. diffusion coefficient of one node (Fig. 5(b)) or catalytic support across a few links (Fig. 5(c)). This 'local strategy' has the important meaning for the control scheme on networks (control process has been an attractive topic to many research groups [17,18,19,20], but controlling networks is not such an explored field yet) and reflects the self-structuring nature of the autocatalytic network.

However, the above work does not guarantee that single-cyclic sub-structure is always selected as a final fittest community. In fact we found that spiral pattern is unstable under the presence of the flat generated by a short hypercycle of 2 or 3 species (flat is stationary spatial-structure dominated by few, less than 3 species). For example, if we assign the catalytic support from species 3 to species 7 in Fig. 5(a) the simple structure in Fig. 6(a) outcompetes other sub-structures in Fig. 5(a). The parasite-like species 2 in Fig. 6(a) survives because the flat generated by a short hypercycle cannot effectively drive away its parasites contrary to the spiral generated by a long hypercycle. This is consistent with the observation of Boerlijst and Hogeweg that a short cycle with dangled parasites frequently emerges from randomly connected structures [8].

The fact that the flat generated by 2 or 3 species outcompetes the spiral generated by more species conflicts with the information-threshold crossing introduced in Section 1. It is unnatural that short cycles are the fittests in prebiotic evolution.

Let us consider the structure assigning the catalytic support from species 5 to species 6 in the structure of Fig. 5(a). Then two sub-structures are emerging; one is the short cycle with a parasite as expected (see Fig. 6(b)), and the other is the composite structure (see Fig. 6(c)) which can be separated into two structures as in Fig. 6(d).

We find that species 5 in the structure of Fig. 6(c) is eventually eliminated, and the flat formed by the short cycle in Fig. 6(b) is outcompeted by the spiral in Fig. 6(c) (see Figs. 7(a) and (b)). At the initial stage, the flat is rapidly

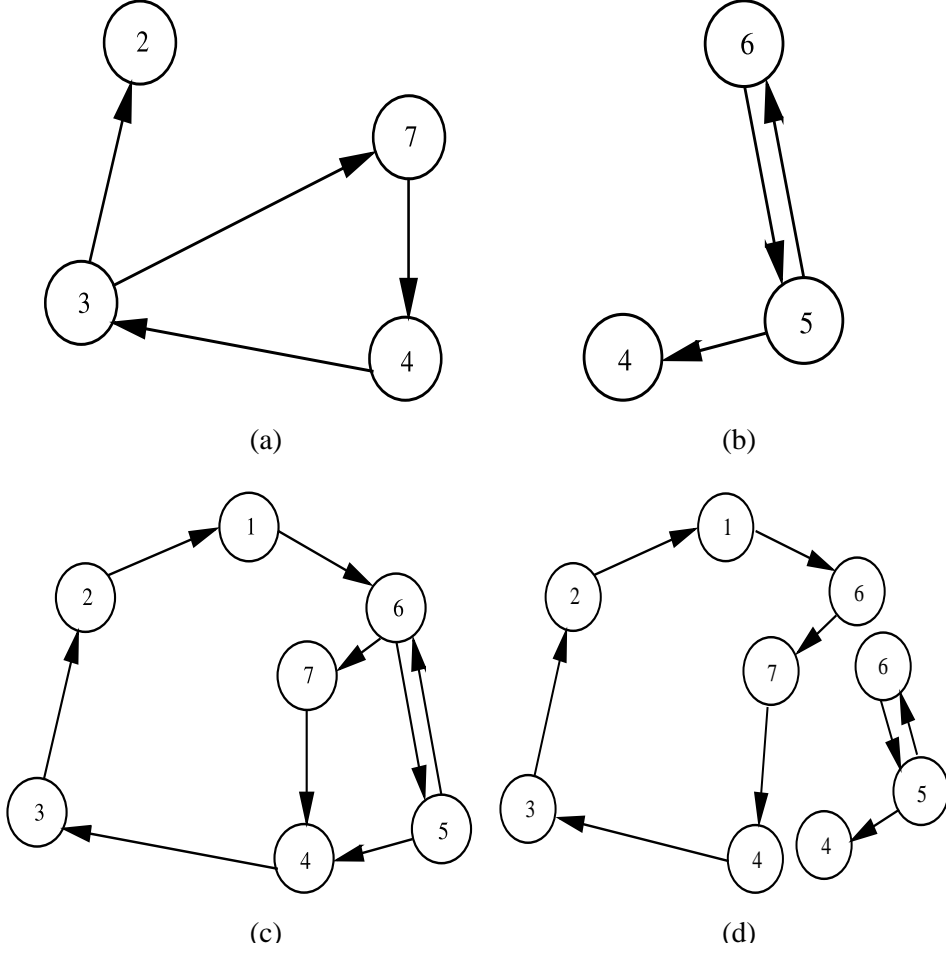


Fig. 6. (a) The fittest structure when we assign the catalytic support from species 3 to species 7 in Fig. 5(a). (b–c) Emergent sub-structures when assigning the catalytic support from species 5 to species 6 in Fig. 5(a). (d) The composite structure in (c) consists of two sub-structures. Community with $6 \rightleftharpoons 5 \rightarrow 4$ is buried in the spiral formed by $1 \rightarrow 6 \rightarrow 7 \rightarrow 4 \rightarrow 3 \rightarrow 2 \rightarrow 1$.

expanded and surrounds the spiral. The flat protects the spiral from the outside environment, otherwise the environment may intimidate the spiral to be extinct. This ‘hypercycle hybrid’ between spiral and flat state is maintained until the spiral becomes fully developed and then the flat is outcompeted by the spiral.

Here we present how the hypercycle hybrid emerges from the complex structure. A short cycle cannot suppress its parasites by the mechanism of spiral-formation. These dangling parasites weaken the activity of the short cycle, thus the short cycle cannot outcompete the long hypercycle containing these parasites. For example, species 4 and 7 in Fig. 6(c) are not driven away by the cycle composed of species 5 and 6, so the hypercycle hybrid can exist as we described above.

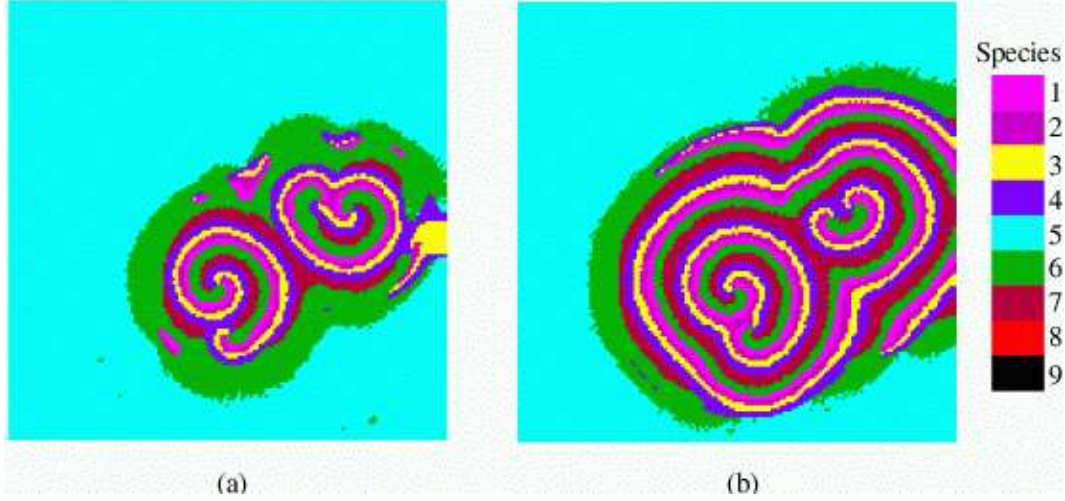


Fig. 7. Hypercycle hybrid between spiral from the structure in Fig. 6(c) and flat from the short cycle in Fig. 6(b) at (a) $t = 100$ and (b) $t = 200$. At the final stage the flat is outcompeted by the spiral completely.

As a consequence a hypercycle hybrid emerges naturally by the short cycle with its parasites, and the hypercycle hybrid provides the selective advantage to the long hypercycle by protecting its early growth process from the environmental species. Selection process on hypercycle hybrid is also expected as previously demonstrated in the case of pure hypercycles in Fig. 5(b) and (c).

4 Maintenance of Communities

After communities are developed completely, interaction between communities becomes an important factor to determine the evolutionary direction of the communities. Let us consider interaction between two emergent hypercycles; cycle A ($1 \rightarrow 2 \rightarrow 3 \rightarrow 4 \rightarrow 5 \rightarrow 6 \rightarrow 1$) and cycle B ($1 \rightarrow 2 \rightarrow 7 \rightarrow 5 \rightarrow 6 \rightarrow 1$) in Figs. 8(a) and (b). We find that cycle B outcompetes cycle A in the long time limit. One difference between these two cycles is the number of species in the cycles, however we found that length of the cycle is not responsible for this outcompetition. For example, if we consider another cycle C ($7 \rightarrow 8 \rightarrow 9 \rightarrow 10 \rightarrow 11 \rightarrow 7$) in Fig. 8(c) instead of cycle B, it turns out that they cannot outcompete each other even though length of cycle C is shorter than that of cycle A. The important difference between these two cases is that cycle A and C are disjoint while cycle A and B are interrelated via several species (in this case, species 1, 2, 5, 6). It turns out that the reason why cycle B outcompetes cycle A is related with this coupling between two hypercycles. More specifically we observe that population of species 4 is markedly decreased when two kinds of spirals come in contact with each other; at the boundary between two spirals, species 5 bred by the short catalysis path

across the species 7 (cycle B) suppresses the population of species 4, which brings the elimination of cycle A.

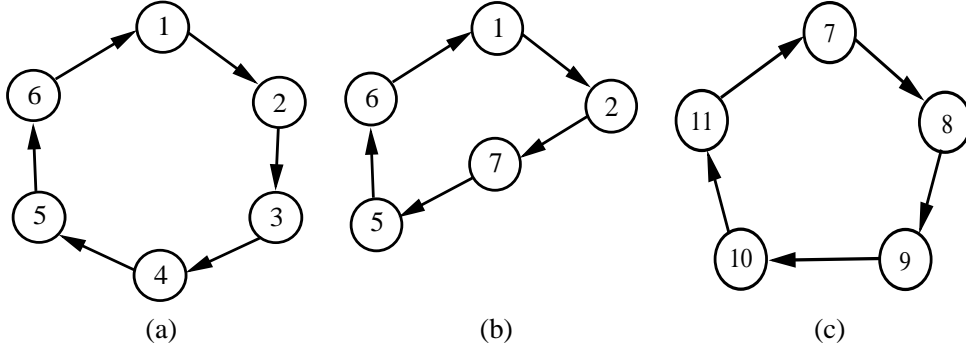


Fig. 8. Interrelation between communities toward different dynamical consequences. Cycle (a) and (b) are interrelated via species 1, 2, 5, 6. In contrast, cycle (a) and (c) are completely disjoint.

The above observation can be interpreted as follows. If there is no shared species/information between two communities (like cycle A and C), nature prefers to conserve information by keeping two communities alive together. However, if there is shared information (like cycle A and B), nature prefers to select specific information rather than conserve information.

From the case between cycle A and C, we notice that conservation of information is obtained by the equivalent competition between spirals rather than by cooperation between spirals. The community based on a spiral is maintained by dynamic process at its core, thus cooperation at the spiral peripheries does not provide any qualitative changes to this system. Therefore a spiral has little selective advantage when maintaining coexistence with other spirals. This property imposes the possibility of the outcompetition between spirals causing a negative effect on information diversity.

There are several ways to diversify genetic information. First, we can allow an evolutionary change of species' character under the competitive ecological condition. Imposed mutation at the spiral core can be effective in this respect. In the spiral core, replication of molecules occurs in an active manner expected to cause a number of mutations, and mutants in the spiral core are not easily outcompeted than mutants in the spiral peripheries [4]. Second, we can compartmentalize the information, which was originally proposed to solve the parasite problem in the hypercycle theory [2,21]. Boerlijst and Hogeweg also showed that compartmentation obtained by spatial gradient of molecular decay rate increases the capacity for information accumulation [13]. Each spiral in its own compartment has to overcome the surrounding barriers in order to compete with the spirals in other compartments, thus resulting in the suppressed competition. Third, we can try endosymbiosis of information. Endosymbiosis means that a symbiont dwells within the body of its symbiotic

partner. For the best known example, Margulis noted that the main internal structures of cells such as mitochondria did not originate inside the cell, but reflect an endosymbiotic coupling [22]. She showed that the basic path of biological evolution is through the symbiosis of independent forms into more efficient and more adaptive cooperatives. We investigate the case by endosymbiosis of information in the next section.

5 Innovation of Communities

As presented in Section 4 spirals showing selfish behavior discourage inheritance of diverse information. Here we investigate one possible solution to increase information diversity in the hypercycle systems. According to Section 2, when a parasite invades spirals the result is either of the followings. The parasite outcompetes spirals or the spirals drive away the parasite depending on choice of parameters. What happens if the parasites which were considered to be toxic to the spirals can catalyze i.e. give some benefit to some species of them?

Given the structure in Fig. 1(a), we increase the diffusion coefficient and rate of catalyzed replication of species 7 high enough to invade the spiral easily. Due to the enhancement the species 7 will outcompete the spirals. However, if we introduce relatively weak catalytic support from species 7 to species 1, symbiosis between the spirals and their parasites is acquired (see Figs. 9(a–c)).

The endosymbiosis over the communities is obtained by the horizontal transfer of parasites. The retrovirus and transposon are examples of the movable genes which are important in the history of evolution [23]. In this respect, one can suspect that it is necessary for the movable genes to show the ‘parasitic’ behavior. If we increase the catalytic support from species 7 to species 1 by $\kappa_{1,7} = 500$, the species 7 fails to invade the spirals. Therefore, the parasitic behavior is necessary for the movable genes to be in symbiosis with spirals.

However, because of the parasitic behavior of species 7, the original species of spirals are having difficulties such that the population becomes depressed (see Fig. 9(d)). Nevertheless, there is a benefit given to the spirals in the symbiosis with species 7. That is, let us consider another species 8 which has the same properties as the species 7 except that it does not catalyze any species in the spirals. Invasion of species 8 would be very toxic to the spirals without species 7, but with the help of the symbiosis with species 7 the spirals can drive away species 8 (see Figs. 10(a) and (b)), i.e. species 7 acts like ‘vaccine’ against the invasion of species 8. This effect originates from the competition between species 7 and species 8. We suppose that this vaccine effect might be

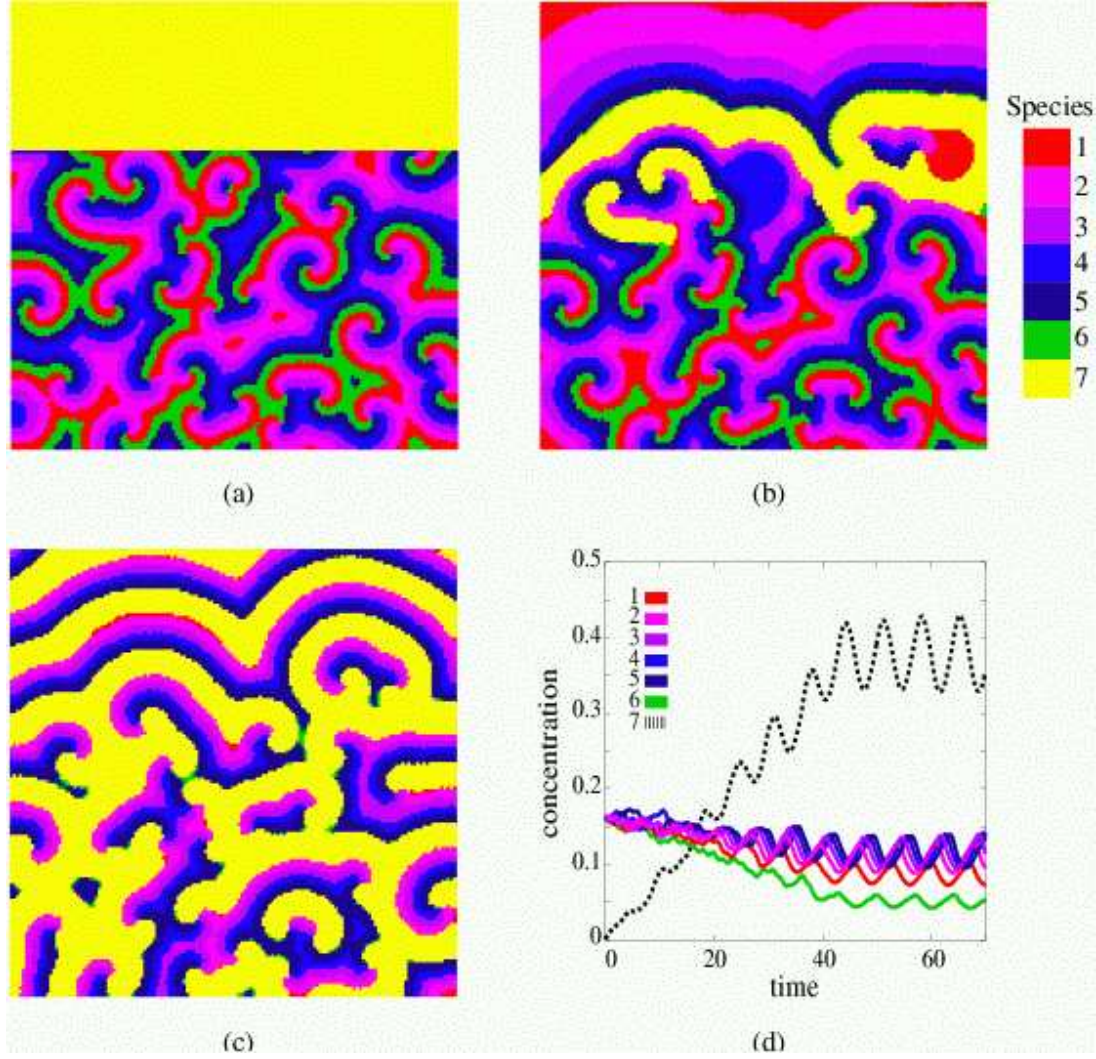


Fig. 9. When a parasite gives weak catalytic support to the hypercycle, endosymbiosis between the hypercycle and its parasite is obtained. Parameter $D_7 = 2$, $\kappa_{7,6} = 1000$, $\kappa_{1,7} = 100$ are used. (a) At $t = 0$, invasion of parasite was set from the top of developed spirals [15]. (b) At $t = 10$, horizontal transfer of parasites. (c) At $t = 100$, endosymbiosis between the hypercycles and their parasites. (d) Concentration of each species as a function of time. The horizontal axis is for evaluation time, the vertical axis for concentration of species averaged over the area occupied by the spirals.

responsible for the prebiotic immunology that should be much simpler than immunology of the present day [24].

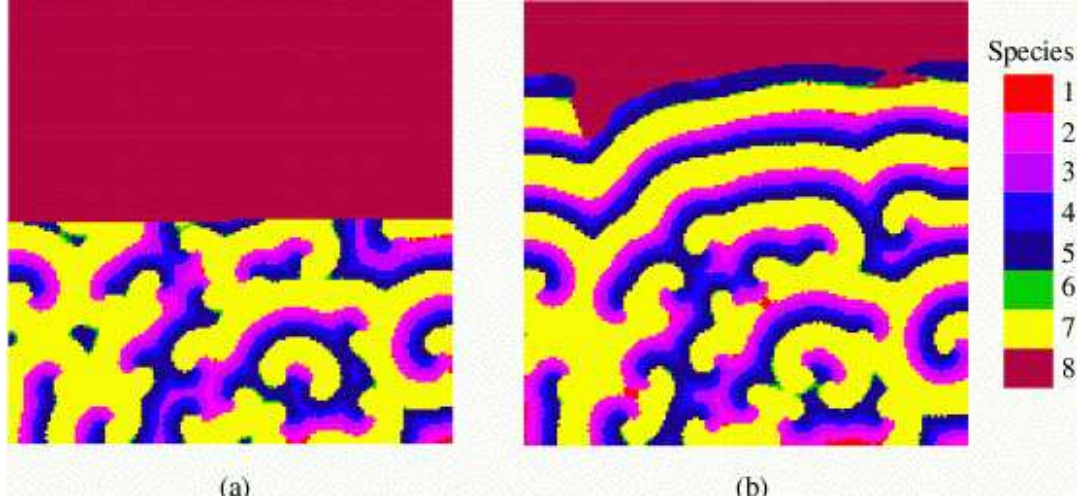


Fig. 10. Demonstration of vaccine effect (refer to the text). (a) Invasion of species 8 from the top of Fig. 9(c) at $t = 0$ [15]. (b) At $t = 50$, the symbiotic unions are driving species 8 away. At the final stage species 8 is completely outcompeted.

6 Conclusion

We have studied spatio-temporal dynamics on the prebiotic evolution of genetic information. In this paper we have investigated emergence, maintenance, and innovation of the information communities. We recognize that symbiosis is important on selection process in prebiotic evolution; the short cycle which consists of only few symbionts fails to organize resistant structure against parasites invasion. However, this helps the emergence of hypercycle hybrid providing the selective advantage for a long hypercycle. Endosymbiosis between a hypercycle and its parasite shows interesting vaccine effect. It is found that this symbiotic union is robust against the invasion of pure parasite.

Self-structuring of species by the complex interaction network leads to the separation of cyclic sub-structures. To select a particular sub-structure we only need to control local properties of the network rather than overall properties of the entire specific sub-structure. The integrity of each sub-structure reflects the emergent property from the collective autocatalytic individuals.

The essential feature of autocatalysis is independent of its precise biochemical definition. Therefore, study on autocatalysis would also be applicable to several area including ecosystems, immune systems, and social networks. We also want to emphasize that the role of self-structuring is not restricted to the specific field – prebiotic evolution. Self-structuring shows various phenomena unexpected by our intuition based on simple ordinary differential equations. In fact, rich nontrivial results are reported [4,5,6,7,25,26,27] in theoretical ecology. Therefore we believe that our work can be of interest in many fields as well.

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- [14] The specific parameters were selected because they belong to the parameter region in which hypercycles can be properly developed and outcompete their initially embedded parasites. See Section 2 for more detail.
- [15] Instead of replacing the existing species by the invading species, we also tried the randomly distributed invading species at that place to imitate more realistic situation. The identical results are reproduced, probably by the partial differential equation nature which promotes the discretized concentration to be flattened. Somewhat different results may be possible in the cellular automata.
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